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Weed reproduction model parameters may be estimated from crop yield loss data

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Studies quantifying weed seed production as a function of weed density are expensive and difficult, and lack of these data is a common limitation in modeling weed population dynamics over time. Observed empirical and theoretical relationships between crop yield loss curves and weed seed production curves led us to the hypothesis that there should be a strong relationship between the shapes of these two curves. Data from literature sources were evaluated to test this hypothesis for hyperbolic curves and to determine if the data describing the crop yield loss caused by weeds could provide estimates of the shape parameter of a hyperbolic equation for describing density dependence in weed reproduction. For each of 162 data sets, a shape parameter ($N50$) and a scale parameter (U) were estimated for an increasing hyperbolic model both for absolute crop yield loss as a function of weed density ($N50_{YL}$, U_{YL}) and for weed yield (either total biomass yield or seed yield) as a function of weed density ($N50_{WY}$, U_{WY}). $N50_{YL}$ was strongly correlated with $N50_{WY}$ across all data sets, with an apparent 1:1 relationship between the two. This relationship suggests that the shape parameter of the yield loss model may substitute for the shape parameter of a hyperbolic model describing the density-dependence of weed seed production. This substitution will be most useful in weed population modeling situations where data describing crop yield loss as a function of weed density are already available, but data describing weed seed production as a function of weed density are not available.

Nomenclature: barnyardgrass, *Echinochloa crus-galli* (L.) Beauv. ECHCG; black medic, *Medicago lupulina* L. MEDLU; catchweed bedstraw, *Galium aparine* L. GALAP; common cocklebur, *Xanthium strumarium* L. XANST; common ragweed, *Ambrosia artemisiifolia* L. AMBEL; corn poppy, *Papaver rhoeas* L. PAPRH; downy brome, *Bromus tectorum* L. BROTE; eastern black nightshade, *Solanum ptycanthum* Dun. SOLPT; field violet, *Viola arvensis* Murr. VIOAR; giant foxtail, *Setaria faberi* Herrm. SETFA; green foxtail, *Setaria viridis* (L.) Beauv. SETVI; hemp sesbania, *Sesbania exaltata* (Raf.) Rydb. ex A.W. Hill SEBEX; johnsongrass, *Sorghum halepense* (L.) Pers. SORHA; jointed goatgrass, *Aegilops cylindrica* Host AEGCY; kochia, *Kochia scoparia* (L.) Schrad. KCHSC; littleseed canarygrass, *Phalaris minor* Retz. PHAMI; redstem filaree, *Erodium cicutarium* (L.) L'Her. ex Ait. EROCI; round-leaved mallow, *Malva pusilla* L. MALNE; smooth pigweed, *Amaranthus hybridus* L. AMACH; spurred anoda, *Anoda cristata* (L.) Schlecht. NAVCR; velvetleaf, *Abutilon theophrasti* Medicus ABUTH; wild oat, *Avena fatua* L. AVEFA; wild poinsettia, *Euphorbia heterophylla* L. EPHHL; wild-proso millet, *Panicum miliaceum* L. PANMI; barley, *Hordeum vulgare* L.; chili, *Capsicum annuum* L.; dry bean, *Phaseolus vulgaris* L.; field pea, *Pisum sativum* L.; maize, *Zea mays* L.; peanut, *Arachis hypogaea* L.; rye, *Secale cereale* L.; safflower, *Carthamus tinctorius* L.; soybean, *Glycine max* L.; sugarbeet, *Beta vulgaris* L.; sunflower, *Helianthus annuus* L.; tomato, *Lycopersicon esculentum* Mill.; wheat, *Triticum aestivum* L.

Key words: Competition, hyperbolic models, interference, population dynamics, seed production, yield loss.

Predictive models of weed population dynamics are receiving increasing attention in weed science (Cousens and Mortimer 1995). These models may be used as teaching aids (Maxwell and Sheley 1997), as research tools (Jordan et al. 1995), as tactical decision aids for selecting economically optimal weed control treatments (Coble and Mortensen 1992; Cousens 1987), or for long-term strategic farm planning (Canner et al. 1998). Processes determining weed population dynamics include seed production, seed mortality, seedling emergence, and seedling mortality (Cousens and Mortimer 1995). Seedling mortality and seed production are density-dependent processes (Cousens and Mortimer 1995), so weed reproduction models must describe seed production as a function of initial seedling density. But experiments quantifying this relationship are difficult and expensive to perform (Cousens and Mortimer 1995) and have been relatively uncommon. This lack of data complicates the parameterization of weed population models.

Rectangular hyperbolic functions and reciprocal yield equations, which are algebraically interchangeable with hyperbolic functions, have been used for modeling yield as a function of plant density for a wide range of agricultural and naturalized species (Pacala 1986; Shinozaki and Kira 1956; Watkinson 1981; Weiner 1982). The common use of these functions has led to the development of theory about the biological meaning of their parameters (Watkinson 1986; Willey and Heath 1969). As a result, the parameters of hyperbolic functions are more readily interpretable than those of other functions, such as quadratic regression models.

Hyperbolic models may also be used to describe both crop yield as a function of weed density (Cousens 1985a, 1985b) and weed seed production as a function of weed density (e.g., Chikoye et al. 1995; Norris 1992; Zanin and Sattin 1988). When using these models, crop yield per unit area is expected to decrease, approaching a minimum as weed density increases, whereas weed seed yield per unit area is expected to increase, approaching a maximum seed yield level as weed density increases. The biological meaning of hyperbolic models suggests that the competitive ability of a weed should be reflected similarly in the shape of both the yield loss curve and the weed seed production curve. More specifically, we propose that a model of weed seed production per unit area could be partially parameterized using a shape parameter of a crop yield loss curve (e.g., Cousens 1985a). If this were true, it would be easier to model weed population dynamics for many systems for which currently only crop yield loss data are available.

The primary objective of this study is to describe the theoretical and empirical relationships between the shape parameter of hyperbolic weed reproduction curves as functions of weed density and the shape parameter of the associated crop yield loss curves. A secondary objective is to further elucidate the biological meaning of these parameters.

Methods

Relating Crop Yield Loss and Weed Yield

The relationship between crop yield loss and weed yield that we tested can be derived from empirical equations describing crop–weed equations. Although empirical, the equations have biological meaning.

Hyperbolic Models for Crop Yield Loss from Weed Competition

It is well documented that the relationship between crop yield loss and weed density can usually be described with a rectangular hyperbolic model (Cousens 1985a). This model has been used numerous times in studies to quantify the relationship between yield loss and weed density and is often used in weed management decision models. Cousens' (1985a) model describes crop yield per unit area (Yld) as a decreasing function of weed density per unit area ($\mathrm{N_{weed}}$):

$$\mathrm{Yld} = \mathrm{Ywf} \cdot \left[1 - \frac{I \cdot \mathrm{N_{weed}}}{\left(1 + \frac{I \cdot \mathrm{N_{weed}}}{A}\right)} \right] \qquad [1]$$

where Ywf represents the crop yield of the system under weed-free conditions, and I and A are fitted parameters. In this equation, the parameter A represents the upper limit of proportional crop yield loss as weed density approaches infinity, whereas the parameter I can be interpreted as the initial slope of the curve, i.e., the amount of proportional yield loss attributable to a single weed per unit area as weed density approaches 0. There are other equivalent equations for a rectangular hyperbola, which may describe the decreasing crop yield or the increasing crop yield loss with increasing weed density. Interpretation of parameters will vary with the form.

The following simple and general formula describes data that follow an increasing hyperbola:

$$R = U_R \cdot \frac{\mathrm{N}}{N50_R + \mathrm{N}} \qquad [2]$$

where R is the response being described (e.g., plant yield per unit area), U_R is the upper limit of the response R as N approaches infinity, N is the plant density of a species in the system, and $N50_R$ is the density at which 50% of U_R is achieved. This formulation breaks the hyperbolic model into two easily interpreted parameters, with $N50_R$ being a shape parameter that describes the horizontal scale in the same density units as N, and U_R describing the vertical scale in the same response units as R. The quantity $U_R/N50_R$ is the limit of the slope of the curve as N approaches 0. Therefore, as $N50$ increases with a constant U_R, the initial slope of the curve decreases (Figure 1A). As U_R varies while $N50_R$ remains constant, the resulting curves differ only in the scale of the y-axis but will have the same shape (Figure 1B).

Crop yield loss as a function of weed density can be described using a form of Equation 2:

$$\mathrm{YL} = U_{\mathrm{YL}} \cdot \frac{\mathrm{N_{weed}}}{N50_{\mathrm{YL}} + \mathrm{N_{weed}}} \qquad [3]$$

where YL is the absolute yield loss at a given weed density $\mathrm{N_{weed}}$, and the parameters U_{YL} and $N50_{\mathrm{YL}}$ are defined in the same way as U_R and $N50_R$ are defined in Equation 2, with the subscript "YL" indicating that yield loss is the response of interest. Equation 3 is equivalent to Equation 1 when Yld $= \mathrm{Ywf} - \mathrm{YL}$, $U_{\mathrm{YL}} = \mathrm{Ywf} \cdot A$, and $N50_{\mathrm{YL}} = A/I$.

Linear Crop and Weed Yield Replacement

Weeds are believed to reduce the crop yield and produce weed biomass, in part, by usurping some resources that would otherwise be used by crop plants (Spitters and Aerts 1983). Therefore, crop yield loss caused by the presence of weeds should be reflected in increases in total weed biomass. Yield replacement, the relationship between crop yield lost and weed biomass produced, has been observed to be approximately linear (Figure 2; Askew and Wilcut 2001; Baziramakenga and Leroux 1998; Charles et al. 1998; Clewis et al. 2001; Holland and MacNamara 1982; Makowski 1995; Malik et al. 1993; Schroeder 1993; Wilson and Wright 1990; Zanin and Sattin 1988). With linear replacement, over a range of weed densities, weed biomass yield per unit area represents a constant proportion of crop yield loss caused by weeds. This replacement proportion (Pr) can be calculated as weed biomass produced divided by crop biomass lost.

A Simple Relationship Between Weed and Crop Yield

Combining the yield replacement relationship with the crop yield loss equation (Equation 3) results in a simple relationship between weed and crop yield. Specifically, if biomass yield replacement is linear and yield loss approaches

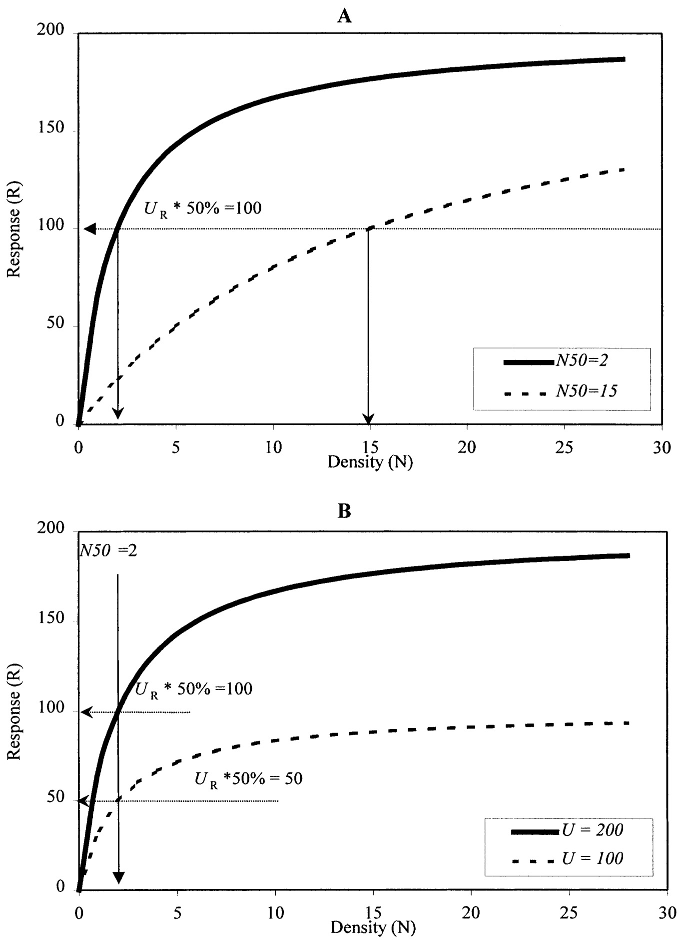

FIGURE 1. Variation in parameter values affects the shape and scale of hyperbolic curves of the form $R = U_R(\mathrm{N}/(\mathrm{N} + N50_R))$, where R is the response being measured, U_R is the asymptotic maximum response level, N is the plant density, and $N50_R$ is the density level where 50% of U_R is achieved. Vertical arrows point to the value of $N50_R$ on the density axis. Horizontal arrows point to the level of 50% of U_R on the response axis. (A) Variation in $N50_R$ affects the shape of curves, without affecting the vertical scale. Both curves have U_R values of 200 but with $N50_R$ values of 2 and 15. (B) Variation in U_R affects the vertical scale of curves, without affecting the shape. Both curves have $N50_R$ values of 2 but with U_R values of 200 and 100.

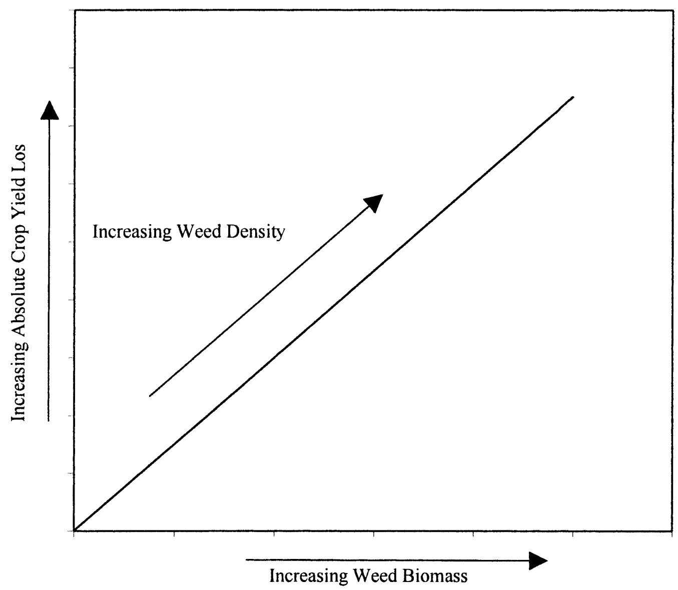

FIGURE 2. Theoretical example of linear yield replacement with crop yield loss approaching 0 as weed biomass approaches 0. The slope of the increasing line indicates the proportion of lost crop biomass that is replaced by weed biomass yield. The linear relationship indicates that both weed biomass and crop yield loss curves will have the same shape when plotted against weed density. The slope is $1/Pr$, where the replacement proportion $Pr = U_{WY}/U_{YL}$.

0 as weed biomass approaches 0 (Figure 2) and if absolute crop biomass yield loss caused by weeds can be described by a hyperbolic model (Equation 3), then weed biomass yield can be described by a hyperbolic model

$$\mathrm{WY} = U_{\mathrm{WY}} \cdot \frac{\mathrm{N_{weed}}}{N50_{\mathrm{WY}} + \mathrm{N_{weed}}} \quad [4]$$

and, more importantly, the hyperbolic model of weed biomass yield will be of the same shape as the crop yield loss model ($N50_{\mathrm{WY}} = N50_{\mathrm{YL}}$) and would differ from the crop yield loss hyperbolic model only by a constant scaling factor Pr (where $Pr = U_{\mathrm{WY}}/U_{\mathrm{YL}}$).

This derived relationship leads to the testable hypothesis that there is an empirical one-to-one relationship between the fitted values of $N50$ for weed yield curves ($N50_{\mathrm{WY}}$; Equation 4) and the fitted $N50$ values for associated crop yield loss curves ($N50_{\mathrm{YL}}$; Equation 3). We test this hypothesis by comparing $N50$ values fitted to previously published experimental data for crop yield loss and weed yield vs. weed density from a range of crops, weeds, climates, and management variables. If the relationship is significant and one-to-one, we propose that the estimated values of $N50_{\mathrm{YL}}$ (Equation 3) for a given situation can be used as "best-guess" estimates of $N50_{\mathrm{WY}}$ (Equation 4) for situations where other data on $N50_{\mathrm{WY}}$ are unavailable.

Estimating Crop Yield Loss *N*50 and Weed Yield *N*50

Data Sets

We used 28 published sources and 1 unpublished source of data containing information about the yields (either seed or total biomass yield) of two species growing in mixture over a range of densities of one of the species. In each pair of species, the species whose density varies is referred to as the "weed," whereas the species whose density is constant is referred to as the "crop." When the density of both species in the experiment is varied in a factorial, the data were analyzed twice, once with each species as the "crop."

The data were organized into "data sets" and "data groups" for analysis. Most of the data sources included several levels of one or more experimental factors, such as sites, years, crop density, irrigation regime, or weed emergence time. A data set is defined as a set of data on crop and weed yield over a range of weed densities from a single experimental treatment, i.e., one combination of the factor levels. A data group is the group of all data sets covering the same crop–weed pair and having the same units of measurement for their yield response variables. For example, a journal article might describe an experiment where a constant crop density is intersown with five densities of weed plants, in a factorial over two different sites and in 2 different yr, and with two different irrigation regimes. Each of the eight

TABLE 1. "Crop" and "weed" species for the 35 data groups used in this study. The "crop" is the species whose density is constant, and the "weed" is the species whose density varies in a data set.

Group ID no.	Crop	Weed
1	Wheat (*Triticum aestivum* L.)	Littleseed canarygrass (*Phalaris minor* Retz.)
2	Maize (*Zea mays* L.)	Barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.]
3	Peanut (*Arachis hypogaea* L.)	Wild poinsettia (*Euphorbia heterophylla* L.)
4	Round-leaved mallow (*Malva pusilla* Sm.)	Redstem filaree [*Erodium cicutarium* (L.) L'Her. ex Ait.]
5	Redstem filaree	Round-leaved mallow
6	Rye (*Secale cereale* L.)	Downy brome (*Bromus tectorum* L.)
7	Green foxtail [*Setaria viridis* (L.) Beauv.]	Safflower (*Carthamus tinctorius* L.)
8	Wheat	Downy brome
9	Maize	Velvetleaf (*Abutilon theophrasti* Medicus)
10	Dry bean (*Phaseolus vulgaris* L.)	Common ragweed (*Ambrosia artemisiifolia* L.)
11	Wheat	Barley (*Hordeum vulgare* L.)
12	Barley	Wheat
13	Barley	Black medic (*Medicago lupulina* L.)
14	Sunflower (*Helianthus annuus* L.)	Kochia [*Kochia scoparia* (L.) Schrad.]
15	Maize	Giant foxtail (*Setaria faberii* Herrm.)
16	Soybean (*Glycine max* L.)	Hemp sesbania [*Sesbania exaltata* (Raf.) Rydb. ex A.W.Hill]
17	Tomato (*Lycopersicon esculentum* Mill.)	Eastern black nightshade (*Solanum ptycanthum* Dun.)
18	Wheat	Jointed goatgrass (*Aegilops cylindrica* Host)
19	Sugarbeet (*Beta vulgaris* L.)	Barnyardgrass
20	Field pea (*Pisum sativum* L.)	Barley
21	Field pea	Barley
22	Peanut	Common cocklebur (*Xanthium strumarium* L.)
23	Soybean	Common cocklebur
24	Green chile (*Capsicum annuum* L.)	Spurred anoda [*Anoda cristata* (L.) Schlecht.]
25	Red chile (*Capsicum annuum* L.)	Spurred anoda
26	Soybean	Smooth pigweed (*Amaranthus hybridus* L.)
27	Soybean	Johnsongrass [*Sorghum halepense* (L.) Pers.]
28	Barley	Wild oat (*Avena fatua* L.)
29	Maize	Wild-proso millet (*Panicum miliaceum* L.)
30	Dry bean (*Phaseolus vulgaris* L.)	Wild-proso millet
31	Wheat	Corn poppy (*Papaver rhoeas* L.)
32	Wheat	Field violet (*Viola arvensis* Murr.)
33	Wheat	Wild oat
34	Wheat	Catchweed bedstraw (*Galium aparine* L.)
35	Maize	Velvetleaf

unique combinations of factors (2 sites by 2 yr by 2 irrigation regimes) becomes one data set, with five weed densities but with no other independent variables within a data set. The eight data sets, though they represent different combinations of factors, become one data group because they all deal with the same crop and the same weed and were measured in the same way. Experiments for a different crop and a weed pair would make up another data group.

A single research article often contributed several data sets from different site-years or from experimental treatments, leading to a total of 35 data groups and 162 data sets. The data groups are described in Tables 1 and 2. In all but one data group (group 8; Table 2), all the data sets in a data group are from the same journal article.

Both weed reproduction modeling and crop yield modeling typically deal with seed production rather than with biomass production. Because seed production is typically roughly proportional to biomass production (Cousens and Mortimer 1995), Equations 1 and 4 are commonly fitted to seed production data and can, thus, yield estimates of $N50$. Although the relationship between $N50_{YL}$ and $N50_{WY}$ could be weaker when using seed production data than when using biomass data, we have treated both types of data equivalently. Available weed yield measurements included total aboveground weed biomass (124 data sets in 25 data groups), weed seed weight (4 data sets in 2 data groups), or weed seed number (34 data sets in 8 data groups). When weed density was measured more than once during the season, the earliest seedling density after crop emergence was used because initial seedling density information is more readily available than mature weed density information for use in weed modeling. In most cases only mean responses to a given weed density were available.

When an article did not include data in tabular form, data were obtained, if possible, by digitally scanning the charts and reading the data point values from their pixel locations. If charts were not available or too crowded to be readable and if the authors had fitted a curvilinear model to describe the data, "pseudodata" were obtained by generating the predicted response values for each weed density in the experiment, using the equations of the fitted curves presented in the article.

Model Estimation Procedures

Two hyperbolic curves (Equation 3 for crop yield loss and Equation 4 for weed yield) as a function of weed density were estimated for each of the 162 data sets. Curve param-

Table 2. Data details by data group.[a]

Group ID no.	Reference	Yield type crop/weed	No. of site-years	Other factors	Total no. of data sets	Maximum weed density	No. of weed density levels	Data extraction method
						m^{-2}		
1	Afentouli and Eleftherohorinos (1998)	r/r	2		2	304	6	DC
2	Bosnic and Swanton (1997)	r/r	2	Two emergence times	8	262	5	DC
3	Bridges et al. (1992)	r/t	2		2	4.4	7–8	DC
4	Blackshaw and Schaalje (1993)	t/t	1	Four crop densities	4	12	5	DC
5	Blackshaw and Schaalje (1993)	t/t	1	Four crop densities	4	12	5	DC
6	Blackshaw (1993a)	t/t	3	Four emergence times	12	400	8	EG
7	Blackshaw (1993b)	t/r	2		2	192	7	DC
8	Blackshaw (1993c)	t/t	3	Four emergence times	12	400	8	EG
8[b]	Blackshaw (1994)	t/t	3	Four wheat varieties	12	200	4	EG
9	Cardina et al. (1995)	r/r	3	Two emergence times by two tillage	10	31	6	EG
10	Chikoye et al. (1995)	r/r	2	Two emergence times	6	12	6	DC–EG
11	Cousens (1985b)	t/t	1	Four crop densities	4	394	5	Tab
12	Cousens (1985b)	t/t	1	Four crop densities	4	353	5	Tab
13	Davidson and Maxwell, unpublished data[c]	t/t	1	Three crop densities	3	398	7	Tab
14	Durgan et al. (1990)	t/t	2		2	7.9	5	Tab
15	Fausey et al. (1997)	r/r	2		2	128	6	DC
16	King and Purcell (1997)	t/t	2	Two harvest dates by two irrigation	8	6	3	DC
17	McGiffen et al. (1992)	r/t	1		1	4.8	5	DC
18	Miller[d]	r/r	1		1	41	5	Tab
19	Norris (1992)	u/t	3		3	133	7–8	DC
20	O'Donovan and Blackshaw (1997)	r/r	2		2	120	5	EG
21	O'Donovan and Blackshaw (1997)	r/t	2		2	120	5	EG
22	Royal et al. (1997)	r/t	4		4	4.4	6	DC
23	Rushing and Oliver (1998)	r/t	1		1	3.3	4	DC
24	Schroeder (1993)	r/t	3	Two emergence times	4	48	6	DC
25	Schroeder (1993)	r/t	3	Two emergence times	4	48	6	DC
26	Toler et al. (1996)	r/t	2	Five densities of a third species	10	3.6	6	Tab
27	Toler et al. (1996)	r/t	2	Five densities of a third species	10	3.6	6	Tab
28	Wille et al. (1998)	r/r	2		2	1,099	5	DC
29	Wilson and Westra (1991)	r/r	2		2	385	5–6	DC–Tab
30	Wilson (1993)	r/r	2		2	110	5	DC
31	Wilson et al. (1995)	r/t	2	Three crop densities	6	636	5	Tab
32	Wilson et al. (1995)	r/t	2	Three crop densities	6	636	5	Tab
33	Wilson and Wright (1990)	t/t	1		1	121	6	DC
34	Wilson and Wright (1990)	t/t	2		2	450	6	DC
35	Zanin and Sattin (1988)	r/t	2		2	80	7–8	EG

[a] Abbreviations: r, reproductive yield; t, total shoot biomass; u, harvested root yield; DC, digitized chart; EG, equation generated; Tab, Tabular or textual data in source.
[b] Data group ID = 8 contains data from two different published sources.
[c] Davidson, R. and B. D. Maxwell. Unpublished data from glasshouse experiment.
[d] Data published on world wide web page: http://www.ianr.unl.edu/jgg/projects/csuwfw.htm.

eters ($N50_R$ and U_R) were estimated using SAS PROC NLIN (SAS 1996). Because "yield loss" cannot be directly measured, parameters of the hyperbolic model for yield loss were estimated directly from crop yield data, using the method of Cousens (1985a), allowing the weed-free yield to be an estimated parameter of the equation:

$$\mathrm{Yld} = \mathrm{Ywf} - U_{\mathrm{YL}} \cdot \frac{\mathrm{N_{weed}}}{N50_{\mathrm{YL}} + \mathrm{N_{weed}}}. \qquad [5]$$

Thirty-four data sets from 13 data groups were discarded from further analysis because for one or both of the response variables, the range of densities was insufficient to fit a complete hyperbolic curve to the data. The discarded data sets are not included in results summary tables.

Testing the Relationship Between Crop Yield Loss *N*50 and Weed Yield *N*50

To test the hypothesis that $N50_{\mathrm{YL}}$ and $N50_{\mathrm{WY}}$ are related in a manner consistent with linear yield replacement, a correlation coefficient was computed for the relationship between the fitted values of $N50_{\mathrm{YL}}$ and $N50_{\mathrm{WY}}$ from all data sets. The values of $N50_{\mathrm{YL}}$ and $N50_{\mathrm{WY}}$ were log transformed for the analysis to improve the normality and homogeneity of variance.

The individual values of $N50_{\mathrm{WY}}$ for all data sets were also regressed against the average $N50_{\mathrm{YL}}$ value of their respective data groups. There were two reasons for using the average value of $N50_{\mathrm{YL}}$ for a data group rather than

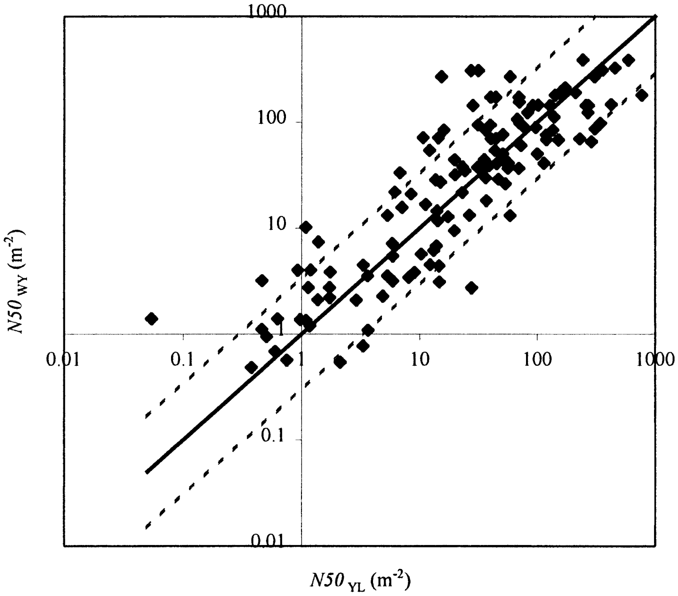

FIGURE 3. Values of $N50_{WY}$ and $N50_{YL}$ plotted by data set. The solid line represents where the two parameters are equal (1:1 line). The dashed lines represent the boundary where $N50_{WY}$ is within a factor of 5 of $N50_{YL}$.

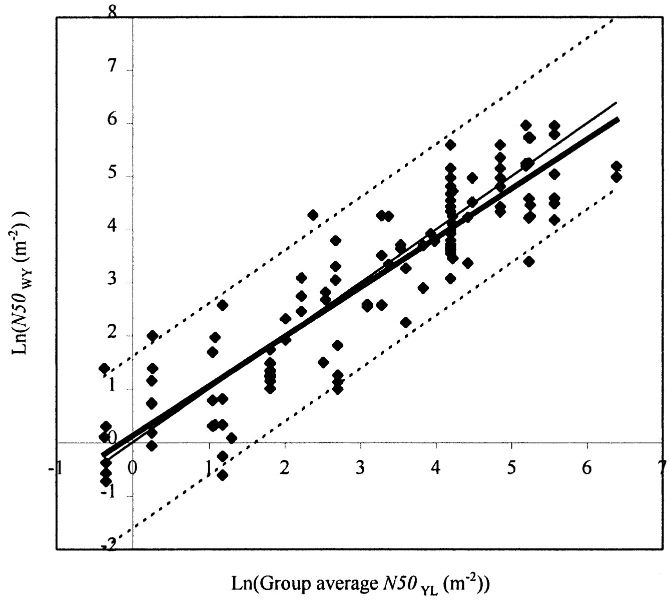

FIGURE 4. Values of $N50_{WY}$ for each data set plotted against the average of $N50_{YL}$ by data group. The heavy solid line gives the regression line $\ln(N50_{WY}) = 0.132 + 0.927 \ln(N50_{YL})$. The light solid line gives the 1:1 line where $N50_{WY} = N50_{YL}$. The dashed lines are the boundary where $N50_{WY}$ is within a factor of 5 of the average $N50_{YL}$, enclosing about 95% of the data points.

the individual values as the independent variable in this regression. First, this regression evaluates using the average $N50_{YL}$ over a range of conditions as a predictor of $N50_{WY}$ because more specific values of $N50_{YL}$ will not generally be available for a modeling situation. Parameters of models typically represent an average value for a range of conditions because modeling the response to specific conditions may be too expensive or time consuming, or the specific condition may not be known in advance for an application of the model. Second, this regression is a more rigorous test of the relationship between values of $N50_{WY}$ and $N50_{YL}$ than a regression between values of $N50_{WY}$ and $N50_{YL}$ from individual data sets. Statistical variability in individual estimates of $N50_{YL}$ violates the regression assumption that the independent variable is not subject to error, and this variability may lead to biased estimates of slope and intercept (Harrison 1990). Using a group average for the independent variable reduces this bias.

The relationship between the two values of $N50$ was explored further by the calculation of the mean, standard error, and correlation of the two values within each data group.

Results and Discussion

Relationship Between Crop Yield Loss *N*50 and Weed Yield *N*50

The log-transformed fitted $N50$ values for yield loss and weed yield from individual data sets showed a positive correlation ($r = 0.84$, $P < 0.0001$; Figure 3). No bias was observed because exactly the same number of points fell on each side of the solid line representing equality between $N50_{YL}$ and $N50_{WY}$. Over half of the $N50_{WY}$ values were within a factor of 2 of their respective $N50_{YL}$ values, whereas 92% of the $N50_{WY}$ values were within a factor of 5 of the $N50_{YL}$ values. This variability is substantial but not too large considering that the $N50_{WY}$ values from all data sets covered a nearly 1,000-fold range, and within a data group (i.e., for a single weed species under varying conditions) the $N50_{WY}$ values differed up to 24-fold.

When the log-transformed values of $N50_{WY}$ from individual data sets in a data group were regressed against the logarithm of the average value of $N50_{YL}$ of the data group, the regression was highly significant with an r^2 of 0.82 ($P < 0.0001$; Figure 4). The slope was not significantly different from 1, and the intercept was not significantly different from 0, indicating a one-to-one relationship between the expected value of $N50_{WY}$ and the group average $N50_{YL}$ and suggesting that in the absence of data for estimating $N50_{WY}$ directly, a general point estimate of $N50_{YL}$ may be an unbiased predictor of values of $N50_{WY}$. When the group average $N50_{YL}$ is used as a predictor of $N50_{WY}$, 95% of the observed values of $N50_{WY}$ fell within a factor of 5 of the predicted value (Figure 4).

The fitted $N50_{YL}$ and $N50_{WY}$ tended to be positively correlated within data groups (Table 3), with all the significant and marginally nonsignificant ($P < 0.20$) correlation coefficients being positive. Although there are several negative correlation coefficients, these are always nonsignificant ($P > 0.20$), suggesting that for those data groups either the number of data sets or the range of $N50$ values may be too small for a strong correlation to be seen.

Biological Meaning of *N*50

Many factors influence the $N50$ parameter, including the environmental conditions and the ecological relationships of the specific species involved. The relative competitiveness of the weed species is an important factor determining the value of $N50$ for a weed species. Low values of $N50$ represent high initial slopes, where weed yield and crop yield loss both

Table 3. Summary by data group of means, standard errors, and correlations for the fitted parameters $N50_{YL}$ and $N50_{WY}$.

Group ID no.	Crop	Weed	n[a]	$N50_{YL}$ Mean (m^{-2})	$N50_{YL}$ (SE)[b]	$N50_{WY}$ Mean (m^{-2})	$N50_{WY}$ (SE)	Correlation r[c]	Correlation P(r = 0)[d]
1	Wheat (*Triticum aestivum* L.)	Littleseed canarygrass (*Phalaris minor* Retz.)	2	600	(170)	160	(16)	1.0	—[e]
2	Maize (*Zea mays* L.)	Barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.]	6	190	(59)	170	(50)	0.18	0.73
3	Peanut (*Arachis hypogaea* L.)	Wild poinsettia (*Euphorbia heterophylla* L.)	2	0.69	(0.23)	2.6	(1.4)	1.0	—
4	Round-leaved mallow (*Malva pusilla* Sm.)	Redstem filaree [*Erodium cicutarium* (L.) L'Her. ex Ait.]	4	470	(160)	120	(25)	−0.31	0.69
5	Redstem filaree	Round-leaved mallow	3	290	(81)	520	(95)	−0.85	0.35
6	Rye (*Secale cereale* L.)	Downy brome (*Bromus tectorum* L.)	11	130	(30)	150	(18)	−0.01	0.97
7	Green foxtail [*Setaria viridis* (L.) Beauv.]	Safflower (*Carthamus tinctorius* L.)	2	34	(11)	39	(1.4)	1.0	—
8	Wheat	Downy brome	24	66	(12)	88	(14)	0.46	0.02
9	Maize	Velvetleaf (*Abutilon theophrasti* Medicus)	10	6.1	(1.4)	3.8	(0.28)	0.58	0.08
10	Dry bean (*Phaseolus vulgaris* L.)	Common ragweed (*Ambrosia artemisiifolia* L.)	5	3.3	(0.87)	3.6	(2.4)	0.64	0.24
11	Wheat	Barley (*Hordeum vulgare* L.)	4	68	(26)	68	(17)	0.92	0.08
12	Barley	Wheat	3	180	(32)	250	(68)	1.0	0.06
13	Barley	Black medic (*Medicago lupulina* L.)	1	51	(—)	50	(—)	—	—
14	Sunflower (*Helianthus annuus* L.)	Kochia [*Kochia scoparia* (L.) Schrad.]	2	1.3	(0.097)	5.7	(1.7)	1.0	—
15	Maize	Giant foxtail (*Setaria faberii* Herrm.)	2	37	(17)	18	(8.5)	1.0	—
16	Soybean (*Glycine max* L.)	Hemp sesbania [*Sesbania exaltata* (Raf.) Rydb. ex A.W.Hill]	2	7.5	(6.4)	8.5	(1.7)	−1.0	—
17	Tomato (*Lycopersicon esculentum* Mill.)	Eastern black nightshade (*Solanum ptycanthum* Dun.)	1	12	(—)	4.5	(—)	—	—
18	Wheat	Jointed goatgrass (*Aegilops cylindrica* Host)	1	11	(—)	71	(—)	—	—
19	Sugarbeet (*Beta vulgaris* L.)	Barnyardgrass	3	2.9	(1.5)	3.0	(1.2)	1.0	0.03
20	Field pea (*Pisum sativum* L.)	Barley	2	29	(15)	49	(21)	1.0	—
21	Field pea	Barley	2	88	(13)	120	(27)	1.0	—
22	Peanut	Common cocklebur (*Xanthium strumarium* L.)	4	0.70	(0.15)	0.77	(0.20)	0.90	0.10
23	Soybean	Common cocklebur	1	3.7	(—)	1.1	(—)	—	—
24	Green chile (*Capsicum annuum* L.)	Spurred anoda [*Anoda cristata* (L.) Schlecht.]	3	14	(3.3)	31	(6.9)	0.94	0.22
25	Red chile (*Capsicum annuum* L.)	Spurred anoda	3	27	(16)	39	(17)	−0.67	0.53
26	Soybean	Smooth pigweed (*Amaranthus hybridus* L.)	5	1.3	(0.44)	1.9	(0.40)	0.02	0.97
27	Soybean	Johnsongrass [*Sorghum halepense* (L.) Pers.]	2	3.0	(2.9)	4.3	(2.9)	1.0	—
28	Barley	Wild oat (*Avena fatua* L.)	2	260	(190)	240	(86)	1.0	—
29	Maize	Wild-proso millet (*Panicum miliaceum* L.)	2	22	(4.5)	13	(0.22)	1.0	—
30	Dry bean (*Phaseolus vulgaris* L.)	Wild-proso millet	2	46	(9.1)	29	(11)	1.0	—
31	Wheat	Corn poppy (*Papaver rhoeas* L.)	4	260	(120)	160	(76)	0.87	0.13
32	Wheat	Field violet (*Viola arvensis* Murr.)	3	190	(82)	150	(76)	−0.94	0.22
33	Wheat	Wild oat	1	54	(—)	44	(—)	—	—
34	Wheat	Catchweed bedstraw (*Galium aparine* L.)	2	83	(63)	49	(20)	1.0	—
35	Maize	Velvetleaf	2	13	(1.4)	16	(1.1)	−1.0	—

[a] "n" is the number of data sets for which $N50$ could be estimated for both crop yield loss and weed yield.
[b] "SE" is the standard error of the mean that cannot be calculated for $n < 2$.
[c] "r" is the correlation coefficient between the yield loss parameter and the weed yield parameter. Cannot be calculated for $n < 2$.
[d] "P(r = 0)" is the approximate probability for the null hypothesis that the true correlation is zero. Cannot be calculated for $n < 3$.
[e] "—" denotes statistics that cannot be calculated because n value was too small.

TABLE 4. Average $N50$ for each data group in the study, sorted by $N50$ value.

Group ID no.	Crop	Weed	$N50$
			m^{-2}
22	Peanut (*Arachis hypogaea* L.)	Common cocklebur (*Xanthium strumarium* L.)	0.74
26	Soybean (*Glycine max* L.)	Smooth pigweed (*Amaranthus hybridus* L.)	1.6
3	Peanut	Wild poinsettia (*Euphorbia heterophylla* L.)	1.6
23	Soybean	Common cocklebur	2.4
19	Sugarbeet (*Beta vulgaris* L.)	Barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.]	2.9
10	Dry bean (*Phaseolus valgaris* L.)	Common ragweed (*Ambrosia artemisiifolia* L.)	3.4
14	Sunflower (*Helianthus annuus* L.)	Kochia [*Kochia scoparia* (L.) Schrad.]	3.5
27	Soybean	Johnsongrass [*Sorghum halepense* (L.) Pers.]	3.6
9	Maize (*Zea mays* L.)	Velvetleaf (*Abutilon theophrasti* Medicus)	4.9
16	Soybean	Hemp sesbania [*Sesbania exaltata* (Raf.) Rydb. ex A.W.Hill]	8.0
17	Tomato (*Lycopersicon esculentum* Mill.)	Eastern black nightshade (*Solanum ptycanthum* Dun.)	8.4
35	Maize	Velvetleaf (*Abutilon theophrasti* Medicus)	14
29	Maize	Wild-proso millet (*Panicum miliaceum* L.)	18
24	Green chile (*Capsicum annuum* L.)	Spurred anoda [*Anoda cristata* (L.) Schlecht.]	23
15	Maize	Giant foxtail (*Setaria faberii* Herrm.)	27
25	Red chile (*Capsicum annuum* L.)	Spurred anoda [*Anoda cristata* (L.) Schlecht.]	33
7	Green foxtail [*Setaria viridis* (L.) Beauv.]	Safflower (*Carthamus tinctorius* L.)	37
30	Dry bean	Wild-proso millet (*Euphorbia heterophylla* L.)	38
20	Field pea (*Pisum sativum* L.)	Barley	39
18	Wheat (*Triticum aestivum* L.)	Jointed goatgrass (*Aegilops cylindrica* Host)	41
33	Wheat	Wild oat (*Avena fatua* L.)	49
13	Barley (*Hordeum vulgare* L.)	Black medic (*Medicago lupulina* L.)	51
34	Wheat	Catchweed bedstraw (*Galium aparine* L.)	66
11	Wheat	Barley	68
8	Wheat	Downy brome (*Bromus tectorum* L.)	77
21	Field pea	Barley	100
6	Rye (*Secale cereale* L.)	Downy brome	140
32	Wheat	Field violet (*Viola arvensis* Murr.)	170
2	Maize	Barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.]	180
31	Wheat	Corn poppy (*Papaver rhoeas* L.)	210
12	Barley	Wheat	220
28	Barley	Wild oat	250
4	Round-leaved mallow (*Malva pusilla* Sm.)	Redstem filaree [*Erodium cicutarium* (L.) L'Her. ex Ait.]	300
1	Wheat	Littleseed canarygrass (*Phalaris minor* Retz.)	380
5	Redstem filaree [*Erodium cicutarium* (L.) L'Her. ex Ait.]	Round-leaved mallow	410

rapidly approach their maximum values as additional weed plants are added. Conversely, higher values of $N50$ represent systems where each additional weed plant per unit area has a relatively small effect. On the basis of this, we would expect that weed species with low values of $N50$ would be larger and relatively more competitive than weed species with higher values of $N50$.

To evaluate the prediction of a relationship between $N50$ and competitiveness, $N50_{YL}$ and $N50_{WY}$ were averaged to obtain an estimate of the overall $N50$ for each data group (Table 4). In general, large, competitive broadleaf weeds tended to have smaller values of $N50$, whereas most grasses and smaller broadleaf weeds tended toward larger values of $N50$. Robust grasses, such as johnsongrass [*Sorghum halepense* (L.) Pers.], wild-proso millet (*Panicum miliaceum* L.), barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.] (in California sugarbeet [*Beta vulgaris* L.]), and giant foxtail (*Setaria faberi* Herrm.) tended to have lower values of $N50$ than did smaller grasses, such as jointed goatgrass (*Aegilops cylindrica* Host.), wild oat (*Avena fatua* L.), barley (*Hordeum vulgare* L.), downy brome (*Bromus tectorum* L.), and wheat (*Triticum aestivum* L.). The low $N50$ for barnyardgrass from group 20, growing in California sugarbeet, may be, in part, because sugarbeet is relatively noncompetitive compared with other crops mentioned in the list. Also, the barnyardgrass in that study was noted to be substantially more competitive than had previously been recorded for that species (Norris 1992).

Application and Utility

Predictions of weed seed production at a given weed density are a critical element of most applications of models of weed population dynamics. Appropriate data to estimate a relationship between weed seed production and weed density are often not available and are costly to obtain because numerous field plots are required to cover the full range of weed densities. Our results suggest a less costly method for modeling weed seed production. Weed seed production can be modeled with a rectangular hyperbola (Equation 4). An estimate of $N50_{WY}$ may be obtained by using a mean value of $N50_{YL}$ estimated from the existing experimental data showing the effect of varying weed densities on crop yield loss. The scale parameter U_{WY} may be estimated using seed yield data from just a single high density of weeds. Using this approach is not complicated; the rectangular hyperbola is a familiar function for modeling both crop yield loss (Cousens 1985a) and weed yield (Chikoye et al. 1995; Norris 1992; Zanin and Sattin 1988), applying the empirical one-to-one relationship between $N50_{WY}$ and $N50_{YL}$ is straightforward, and the relationship has a simple biological interpretation.

The positive correlations between individual data set values of $N50_{WY}$ and $N50_{YL}$ within data groups (Table 3) suggest that when a more specific estimate of $N50_{YL}$ is possible for a given modeling situation, that value may also be used as a specific estimate of $N50_{WY}$. This may be useful when the modeler wishes to use an estimate of $N50_{YL}$ that differs from the average $N50_{YL}$, such as when there is prior knowledge about future growing conditions (e.g., macroclimatic forecasts, management variables, or site-specific variables) or when performing risk-assessment modeling.

Reasonable estimates of $N50$ may even be obtained from expert opinion because the parameter is biologically interpretable. If a given crop–weed combination has not been studied and estimates of $N50_{YL}$ from data are not available, subjective information about the relative "competitiveness" of the crop and weed may be used to obtain a best-guess estimate of $N50$ that will apply to both yield loss and weed yield. This method has been useful in developing a multiple-weed, multiple-crop model that includes weed–crop combinations that have not previously been studied (Canner et al. 1998).

When a value of $N50_{WY}$ is estimated by substituting the expected value of $N50_{YL}$, our results suggest that the actual value of $N50_{WY}$ for a given situation will tend to fall within five times greater than or less than the estimated value (Figure 4). The magnitude of this potential error may seem unacceptably large for using this method for predicting the seed production. But the prediction accuracy associated with this method may be comparable to that of other methods currently used to select parameters of models of weed population dynamics. Accurate prediction of seed production is difficult because seed production curve parameters are highly variable under different environmental and management conditions. For example, values of $N50_{WY}$ estimated directly from the weed yield data used in this study commonly varied by at least twofold and by as much as 24-fold between different growing conditions and management systems (data sets) for a given crop–weed pair (data group). In any practical modeling application requiring prediction of weed seed production under unknown future conditions, there will be error associated with the use of any single value of a curve parameter such as $N50_{WY}$ regardless of the source of that value. Furthermore, the modeler must evaluate the sensitivity of a model's outputs to variation in $N50_{WY}$ because large variation in $N50_{WY}$ does not always lead to similarly large variation in predictions of weed seed production. Thus, this method of parameter selection may provide results that are within acceptable limits for a given application.

The substitution of $N50_{YL}$ for $N50_{WY}$ provides a means to model a critical component of weed population dynamics when data on density-dependent weed seed production are not available. The utility of applying our suggested $N50$ substitution in a model will depend on a number of factors, including the risks and benefits associated with a given level of accuracy in the modeling application and the costs of another more accurate modeling method and its required data. This simple method may be most useful in weed population modeling where the required accuracy is relatively low, but where data are not available and the costs of developing a more accurate method are large. In many applications the use of the $N50$ substitution could be preferable to the alternative of leaving a weed out of the model entirely.

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